Critical Weights of Boll Weevil (Coleoptera: Curculionidae) Larvae in Relation to Square Desiccation and Natural Mortality

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ABSTRACT Starvation of immature boll weevils resulting from square desiccation is considered a major determinant of natural mortality. However, the critical weight below which a larva cannot complete development without further feeding has not been determined. Critical weights of second and third instars were investigated using food-removal techniques, and the age and size distributions of larvae in newly abscised squares were estimated from field collections. Second instars examined averaged 3.22 mg in weight and ranged from 0.23 to 5.55 mg. About 80% of second instars weighing ≥1.67 mg molted, but none pupated. The estimated critical weight for 50% of unfed second instars to survive to third instar was 2.49 mg. Third instars examined averaged 14.64 mg in weight and ranged from 1.81 to 34.43 mg. About 64% of third instars weighing ≥5.29 mg developed into adults, ranging in weight from 1.61 to 21.49 mg and averaging 10.44 mg. Estimated critical weights for 50% of unfed third instars to survive to the pupal and adult stages were 6.63 and 8.89 mg, respectively. The estimated critical weight for 50% of pupae to survive to adulthood was 4.52 mg. Larvae collected from newly abscised squares were predominantly second (56%) and third instars (39%). Furthermore, an estimated 19% of all larvae collected were capable of development to adulthood without further feeding. In light of the rapid rate of larval growth and development, our results suggest that square desiccation sufficient to deter feeding by larvae must occur within 1–3 d of square abscission to produce a high proportion of starvation-induced mortality.

KEY WORDS boll weevil, *Anthonomus grandis grandis*, natural mortality, critical weight

Natural mortality is an important factor limiting growth of populations of the boll weevil, *Anthonomus grandis grandis* Boheman (Smith 1936, Sturm and Sterling 1990, Sturm et al. 1990). However, the underlying mechanisms responsible for natural mortality are not well understood. Both exposure to high temperatures and square desiccation have been identified as causes of natural mortality. DeMichele et al. (1976) and Curry et al. (1982) assumed that desiccation of the larval food supply (squares) rather than exposure to high temperatures was the primary cause of larval mortality. They also assumed that the principle effect of high temperatures on weevil mortality was to hasten square desiccation. Square desiccation sufficient to deter feeding presumably results in larval death unless resources adequate for the completion of development were previously acquired. However, the minimum size or age at which a larva can complete development without further feeding has not been determined.

Fye and Bonham (1970) identified high temperatures as the primary cause of natural mortality. Yet desiccation of the larvae or squares was not measured in their study. Sterling et al. (1990) examined weevils infesting bolls and suggested that high temperatures and desiccation contribute to natural mortality. Because bolls do not commonly abscise in response to boll weevil infestation, those findings do not directly address natural mortality as it occurs in the field.

A clearer understanding of the mechanisms of natural mortality may improve our ability to maximize the deleterious impacts of natural mortality on boll weevil populations. Direct examination of these mechanisms is effectively precluded by the difficulty of independently manipulating temperature, desiccation of the food source, and desiccation of the larva. Alternatively, food-removal techniques may be used to indirectly examine the effects of rapid food deterioration presumed to result from square desiccation. The aim of this approach is to estimate the larval age or size beyond which the likelihood of mortality in response to an inadequate or unpalatable food source diminishes. Our objectives were to determine the respective critical weights necessary for second and third instars to complete development without further feeding, and to estimate the age and size distributions of larvae represented in newly abscised squares.

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Materials and Methods

Critical Weight Determination. Larvae were reared from field-collected, oviposition-punctured squares. Samples of 100–400 infested squares were collected from cotton plants in commercial fields about weekly between mid-July and late-August of 1999 and 2000. Samples were held in screened Plexiglas cages (20 × 20 × 20 cm) in an environmental chamber at 29.4 ± 1°C with photoperiod of 13:11 (L:D) h. About 10 squares from each sample were opened daily to monitor larval development. Larval instar was determined based on head capsule width (unpublished data). When >50% of the squares contained second and third instars, larvae were harvested and individually weighed to the nearest 0.01 mg on an analytical balance (model AT261, Mettler-Toledo, Columbus, OH). Each larva was then placed on a platform constructed of a plastic lid (PL1 snap-on lid, SOLO Cup, Urbana, IL) that was glued upside down in the bottom of a 100 × 15-mm plastic petri plate. Each petri plate contained a cotton wick (≈1 cm long) saturated with deionized water to prevent larval desiccation. Wicks were periodically rewetted. Petri plates were held in the same environmental chamber used to hold infested squares. Larvae were observed at least daily until adult eclosion or death. The stage of development, weight, and the date of observation were recorded for each weevil following each molt unless the larva died.

The influences of larval and pupal weights on survival to subsequent stages of development were assessed by grouping second instars, third instars, and pupae into respective sets of weight classes. Second instars were grouped by weight into six classes with each class spanning 1 mg. Weight classes ranged from 0–1 mg to 5–6 mg. The weights of third instars and pupae were similarly grouped into 35 and 25 1-mg weight classes, respectively. Each respective relationship between weight class and the observed proportion of survival to a subsequent stage was described using a logistic function modified by addition of an intercept term ($Y = \beta_0 + [e^{(\beta_1 + \beta_2 * \text{WEIGHT CLASS})} / (1 + e^{(\beta_1 + \beta_2 * \text{WEIGHT CLASS})})]$), where Y is the proportion of a given weight class surviving to a given instar or stage, WEIGHT CLASS is a given 1-mg larval or pupal weight class, and β_0, β_1, and β_2 are estimated. The logistic functions were fitted to the data by weighted nonlinear regressions using the SAS procedure PROC NLIN (SAS Institute 1988). The fitted logistic functions were then used to estimate the critical weights required for 50% of each respective instar to survive to a subsequent instar or stage in the absence of food (CW_{50}).

The relationships between weights of unfed third instars and respective weights of resulting pupae and adults were estimated by simple linear regressions (PROC REG; SAS Institute 1988). In each regression model, third instar weight was the independent variable, and either pupal weight or adult weight was the dependent variable.

Age and Weight Distributions of Weevils in Fallen Squares. Newly fallen squares were collected from a single field of flowering cotton ('Deltapine 5415') on 8, 11, 15, and 18 August 2000. Three 30-m sample areas each established between two rows (1.02-m row spacing) were prepared for sampling by collecting and discarding all fallen squares and debris 12 h before the first collection of newly fallen squares on each sample date. Collections of fallen squares taken at 0700, 1100, 1500, and 1900 hours CDT on the following day were used to determine the age and weight distributions of square-infesting weevils. Collected squares were placed in sealable plastic bags labeled according to the time and date of collection. Squares were transported to the laboratory and dissected to determine the condition (alive, dead), instar, and weight of each weevil larva.

Age distribution of larvae collected from newly fallen squares was determined by separating the larvae into groups according to instar. Larvae within each instar were further grouped into 1-mg weight classes to estimate the proportion that was capable of completing development to adulthood without further feeding. Predicted survival was estimated by multiplying the number of larvae in a given weight class by the respective proportion of survival to adulthood as estimated by the previously described logistic functions.

Results

Critical Weight Determination. A total of 54 unfed second instars ranging in weight from 0.23 to 5.55 mg were examined. Of these, 43 developed into third instars that ranged in weight from 1.21 to 4.45 mg. The relationship between larval weight class and survival of second instars to the third instar was significant (F = 14,086.7; df = 3, 3; $P < 0.001$; $r^2 = 1.000$; Fig. 1A). The smallest second instar to become a third instar weighed 1.67 mg, and all second instars weighing >3 mg survived to the third instar. The logistic function estimated a CW_{50} of 2.49 mg for second instars (Fig. 1A). No second instars denied food developed to the pupal stage.

A total of 616 unfed third instars weighing from 1.81 to 34.43 mg were examined. Of these, 458 developed into pupae whose weights ranged from 1.62 to 24.48 mg. The smallest third instar to pupate weighed 4.82 mg, and survival of third instars to the pupal stage was dependent on larval weight class (F = 284.52; df = 3, 31; $P < 0.001$; $r^2 = 0.993$; Fig. 1B). The estimated CW_{50} for third instars to develop to the pupal stage was 6.63 mg. The logistic function predicted a maximal proportion of survival of 0.89 (Fig. 1B). This prediction indicated the occurrence of some mortality from causes unrelated to larval weight. Survival of larvae from most weight classes >10 mg were at least 80%, except for an apparent outlier for the 32–33-mg weight class, which was 33% (Fig. 1B). Presence of this outlier did not greatly influence the relationship estimated by the weighted regression because of the small sample size (n = 3) associated with this weight class.

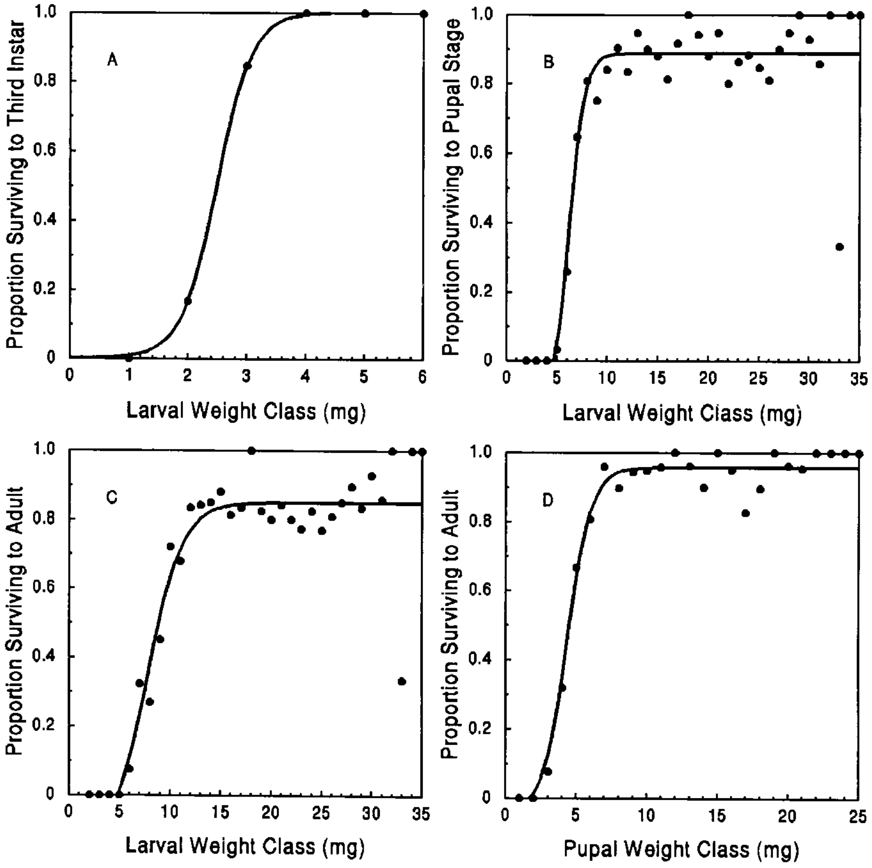

Fig. 1. Modified logistic functions describing the relationships between boll weevil (A) second instar weights and survival to the third instar ($Y = 0.002 + [e^{(-8.281\ +\ 3.326*x)}/(1 + e^{(-8.281\ +\ 3.326*x)})]$), (B) third instar weights and survival to the pupal stage ($Y = -0.112 + [e^{(-8.140\ +\ 1.296*x)}/(1 + e^{(-8.140\ +\ 1.296*x)})]$), (C) third instar weights and survival to adulthood ($Y = -0.150 + [e^{(-4.517\ +\ 0.578*x)}/(1 + e^{(-4.517\ +\ 0.578*x)})]$), and (D) pupal weights and survival to adulthood ($Y = -0.043 + [e^{(-5.119\ +\ 1.171*x)}/(1 + e^{(-5.119\ +\ 1.171*x)})]$), where Y = proportion of larvae or pupae surviving to the designated instar or stage and x = 1 mg larval or pupal weight class.

Survival of unfed third instars to adulthood was lower than survival to the pupal stage, but 393 larvae continued development to produce adults weighing 1.61–21.49 mg. Survival of these larvae to adults was again related to larval weight ($F = 272.52$; df = 3, 31; $P = 0.001$; $r^2 = 0.989$; Fig. 1C), and the estimated CW_{50} was 8.89 mg. The smallest third instar to survive to adulthood weighed 5.29 mg. The logistic function estimated a maximal proportion of survival of 0.85 for larvae weighing >17 mg (Fig. 1C). Thus, background mortality unrelated to larval weight and occurring during development to adulthood was slightly higher than mortality occurring during development to the pupal stage.

The relationship between pupal weight class and survival to the adult stage was also significant ($F = 1{,}144.73$; df = 3, 22; $P < 0.001$; $r^2 = 0.997$; Fig. 1D). The estimated CW_{50} for pupae was 4.52 mg, and the smallest pupa to become an adult weighed 2.72 mg. The logistic function estimated a maximal proportion of survival to the adult stage of 0.96 for pupae weighing >9 mg (Fig. 1D).

Regression analysis indicated a significant positive relationship between third instar and pupal weights ($F = 3{,}333.31$; df = 1, 456; $P < 0.001$; $r^2 = 0.880$; Fig. 2A). Both the intercept of the fitted model (–1.610; SE = 0.249; $t = -6.47$; df = 1, 456; $P < 0.001$) and the coefficient for third instar weight (0.757; SE = 0.013; $t = 57.73$; df = 1, 456; $P < 0.001$) were statistically significant. A similar relationship was detected between third instar weights and the weights of resulting adults ($F = 2{,}110.65$; df = 1, 391; $P < 0.001$; $r^2 = 0.844$; intercept = –1.724; SE = 0.282; $t = -6.12$; df = 1, 391; $P < 0.001$; coefficient for third instar weight = 0.654; SE = 0.014; $t = 45.94$; df = 1, 391; $P < 0.001$; Fig. 2B). Both models were sufficient to explain a large proportion of the variation observed in the data.

Instar and Weight Distributions of Weevils in Fallen Squares. The distribution of weevils instars within newly fallen squares was 5% first instar ($n = 7$),

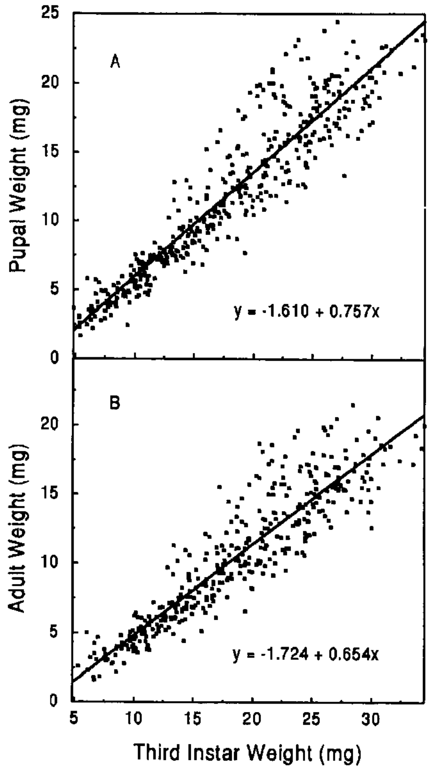

Fig. 2. Relationships between respective weights of unfed third instar boll weevils and resulting (A) pupae and (B) adults.

56% second instar (n = 77), and 39% third instar (n = 53). No eggs, pupae, or adults were found. Of the 141 larvae observed, only four were not alive at the time of collection (one first instar and three third instars). Weights of first instars averaged 0.37 mg and ranged from 0.17 to 0.88 mg; second instars averaged 2.14 mg in weight and ranged from 0.48 to 5.39 mg. Third instars averaged 10.75 mg in weight (range, 1.64–32.52 mg) and 49% were in excess of the estimated CW_{50} (8.89 mg). These larvae represented 19% of the total number of collected larvae. The survival of larvae to adulthood that was estimated from the observed distributions of third instar weights and the corresponding proportions of survival predicted by the logistic equation was also 19%.

Discussion

Although 80% of observed second instars successfully molted in the absence of food, none survived to pupation. These results demonstrate that second instars denied food are unlikely to develop to adulthood. Thus, square desiccation sufficient to deter feeding by first and second instars would result in very high or complete larval mortality. In contrast, many of the third instars survived to the pupal and adult stages despite the absence of further feeding (74 and 64%, respectively).

The practical implications of the relationships between larval weight and survival to subsequent stages can be illustrated in a conceptual model. When observed instar and weight distributions of larvae in newly fallen squares are coupled with stadium estimates of respective instars as reported by Bacheler et al. (1975), the cumulative percentage of larvae attaining the CW_{50} (8.89 mg) as third instars at 28°C can be estimated for different time intervals. Estimates of stadium length at 28°C were obtained by averaging estimates of Bacheler et al. (1975) at 26°C and 30°C. We also assumed that the ages of first and second instars were evenly distributed within respective stadia. The initial percentages of larvae at each instar were determined based on the results of field collections of newly fallen infested squares. The percentages of first and second instars molting by the end of a given time interval were calculated by dividing the elapsed time by the respective stadium duration. Calculations were repeated for each successive time interval until all first and second instars became third instars. Larvae were assumed to enter the third stadium at the minimum weight observed (1.64 mg) for third instars in newly fallen squares. A linear rate of weight gain was assumed for third instars and was represented by an average rate estimated from observed larval weights. This rate was calculated by subtracting the minimum observed weight from the maximum observed weight (32.52 mg) and dividing the difference by the stadium duration. This difference was then divided by the duration of the third stadium. Thus, we estimated an average rate of third instar weight gain of 7.98 mg/d.

The conceptual model predicted that ≈56% of the larval population in newly fallen squares would attain the CW_{50} for third instars by 1 d after square abscission, and ≈90% would attain this weight by 2 d after square abscission. After 3 d, ≈95% of the larvae were predicted to attain the CW_{50} for third instars. Although these estimates are theoretical, they suggest that under weather conditions typical of the cotton production season square desiccation sufficient to prevent larval feeding must occur rapidly (1–2 d) to produce a high proportion of starvation-induced mortality.

Our results question the prominence of square desiccation in determining the levels of natural mortality of boll weevil larvae in the field. However, these findings do not address the potential contribution of larval desiccation and exposure to high temperatures to such mortality. A more complete understanding of the mechanisms controlling natural mortality and the interactions of these mechanisms with the environment will be required to develop crop production practices that maximize these effects on boll weevil populations.

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